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记比耶鱼(*Birgeria*)在中国的首次发现[1)]

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摘要 记述了采自云南罗平晚三叠世法郎组竹杆坡段的比耶鱼一新种——刘氏比耶鱼(*Birgeria liui* sp. nov.),这是比耶鱼化石在中国的首次发现。刘氏比耶鱼与产自瑞士圣乔治山中三叠世边境沥青层的史氏比耶鱼最为相近,两者仅在尾柄长高之比、尾鳍长短与上下叶外缘交角、背鳍和臀鳍辐状支鳍骨的数目、臀鳍辐状骨骨板的大小、以及侧线管骨化与否等特征上略有差异。比耶鱼与软骨硬鳞鱼超目的鲟形目最为接近,两者共有一系列特征,如除尾上叶外体侧裸露,副蝶骨末端伸达头后,鳃盖骨退化;但比耶鱼同时也具有不少的特有特征,代表了软骨硬鳞鱼超目的另一类群——比耶鱼目(Birgeriiformes ord. nov.)。刘氏比耶鱼的发现进一步表明华南扬子区中、晚三叠世鱼类化石与特提斯西部的鱼群具有密切的动物地理关系。

关键词 云南罗平,晚三叠世法郎组,比耶鱼科

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近年来,在贵州的关岭、兴义和云南的罗平等地的中、晚三叠世关岭组和法郎组地层中发现了大量以前未知的海生爬行动物化石,迄今已报道了鱼龙、鳍龙、海龙三类共计9个新属12个新种(Li, 1999, 2000; Liu, 1999; Liu and Rieppel, 2001; Rieppel et al., 2000; Yin et al., 2000)。然而,伴随爬行动物而发现的众多鱼类化石的研究并未得到相应的重视,目前已知的鱼类化石仍仅有苏德造(1959)记述的东方肋鳞鱼(*Peltopleurus orientalis*)、贵州中华真颚鱼(*Sinoeugnathus kueichowensis*)和兴义亚洲鳞齿鱼(*Asialepidotus shingyiensis*)。

本文记述了李淳采自云南罗平法郎组竹杆坡段的比耶鱼化石,这是比耶鱼在中国的首次发现。这一发现对了解华南扬子区中、晚三叠世海相鱼类化石的面貌以及确定古动物地理区系等具有一定的意义。

1 系统记述

硬骨鱼纲 Class Osteichthyes Huxley, 1880

辐鳍鱼亚纲 Subclass Actinopterygii Cope, 1887(sensu Rosen et al., 1981)

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软骨硬鳞鱼超目 Superorder Chondrostei Müller,1844(sensu Patterson,1982)

比耶鱼目(新目) Order Birgeriiformes ord. nov.

比耶鱼科 Family Birgeriidae Aldinger, 1937

比耶鱼属 Genus *Birgeria* Stensiö,1919

刘氏比耶鱼(新种) *Birgeria liui* sp. nov.

(图 1；图版 Ⅰ～Ⅱ)

正型标本 一较为完好的身体后部标本；中国科学院古脊椎动物与古人类研究所标本编号：IVPP V 12569(图 1；图版 Ⅰ～Ⅱ)。

产地和层位 云南罗平长底；晚三叠世卡尼早期法郎组竹杆坡段(据 Wang et al., in press)。

特征 尾柄细长、尾柄长高之比为 2.7，尾鳍强大、上下叶外缘交角 70°，臀鳍的辐状支鳍骨骨板很小，头后侧线管已骨化。

释名 种名谨献予刘宪亭先生(1921～2001)。

描述 目前惟一的标本保存部分长 380mm；从比耶鱼已知种类的身体各部比例推测，这一标本完整时的全长可达 800mm 左右。该标本的体型细长，尾柄长为尾柄高的 2.7 倍；中轴骨骼的脊椎弓片骨化程度较高；背鳍和臀鳍位处身体的后部，背鳍的起点略前于臀鳍；尾鳍叉裂颇深，上、下叶近等长，上下叶外缘交角 70°(图 1；图版 I～II)。

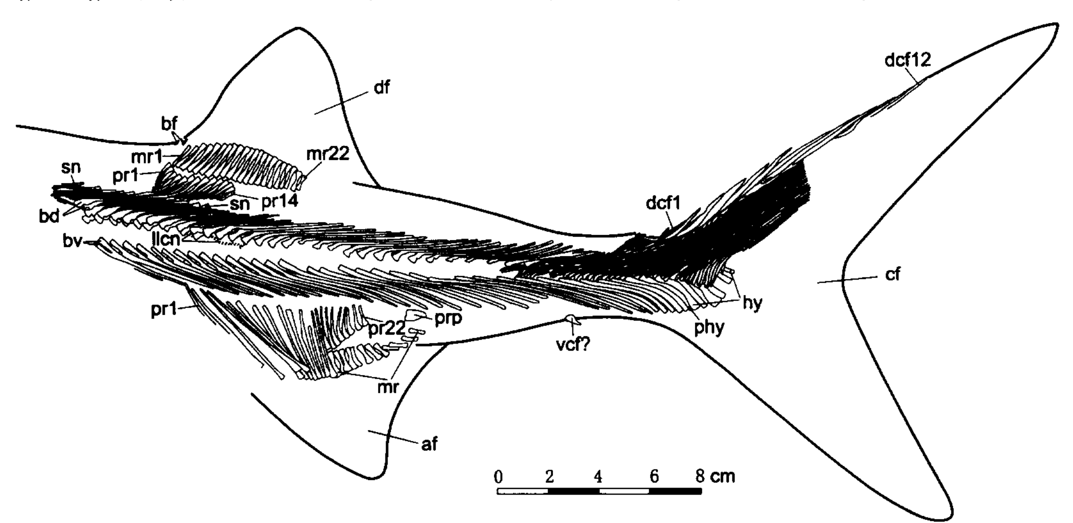


图 1 刘氏比耶鱼(新种)正型标本的线条图(IVPP V12569)

Fig.1 *Birgeria liui* sp. nov., line drawing of the holotype (IVPP V12569)

Abbreviations: af, anal fin: bd, basidorsals; bf, basal fulcra in front of the dorsal fin; bv, basiventrals; cf, caudal fin; dcf, dorsal caudal fulcra; df, dorsal fin; hy, hypurals; llcn, lateral line canal ossifications; mr, middle radials of the dorsal and anal fins; phy, parhypural; pr, proximal radials of the dorsal and anal fins; prp, proximal radial plate of the anal fin; sn, supraneurals; vcf, ventral caudal fulcrum

脊柱 与其他软骨硬鳞鱼类一样，当前标本的脊索仍很完整发达，但环绕脊索的脊椎弓片骨化程度较高，且尾部的绝大多数成对弓片在远端已愈合，形成单一的神经棘和脉

棘，与比耶鱼以外的其他软骨硬鳞鱼明显有别，而类似于新鳍鱼次亚纲(Neopterygii)的鲱口鱼类(Halecostomi)。

当前标本的尾部共有相当于36枚脊椎的弓片成分(尾鳍部分除外)。已骨化的脊椎弓片包括成对的基背片和基腹片，以及尾前部的上神经棘(=上背片)。基背片(bd)的基部膨大，并发育有类似于真骨鱼类髓弓前后关节突的突起。尾前部的10对基背片左右仍彼此分离，并有上神经棘(sn)与之在远端相接；尾后部的每对基背片除基部外已左右愈合，形成细长的神经棘。基腹片(bv)的基部略膨大，形成类似于脉弓的结构。尾部的基腹片每对已大部愈合，向后下方伸长形成脉棘。尾鳍基部的7根脉棘在远端从前往后依次膨大，以支持尾下叶鳍条。

背鳍　背鳍(df)近呈三角形，前缘稍凸，后缘略凹，前缘略短于后缘，后缘与背鳍基大致等长。背鳍最前端有2枚短小的基部棘鳞(bf)，之后为依次加长的10余根分节鳍条。背鳍鳍条总计多于50根。所有鳍条均较细，排列紧密，除基部外分节，节距很长；前缘依次加长的鳍条不分叉，其余鳍条在远端分叉。

当前标本的背鳍后部辐状支鳍骨在标本正负两面劈开时已损失，但前部的近端和中间两列辐状支鳍骨均保存完好。两列辐状骨都为细长的扁棒状骨，但中间辐状骨(mr)的两端膨大、中部略收缩，似哑铃形；近端辐状骨(pr)则仅远端加宽，更似向脊柱方向变细的长楔形。当前标本中保存的近端辐状骨14根，中间辐状骨22根。该标本如完好保存，近端辐状骨系列的后端应有一块由数根辐状骨愈合而成的骨板；中间一列辐状骨的数目则可达30～32根。

臀鳍　臀鳍(af)鳍条在当前标本中大部缺失，但从标本上残存的印痕仍可见臀鳍与背鳍大小相若，外形亦似三角形。臀鳍的前缘略凸，后缘明显内凹呈镰形。臀鳍的鳍条特征亦与背鳍相同，其鳍条数目也应多于50根。

臀鳍的辐状支鳍骨在当前标本中基本保存完好。比耶鱼的臀鳍辐状支鳍骨在已知的软骨硬鳞鱼类中颇为奇特，其内侧的近端辐状骨可分为前后两部分：前部的近端辐状骨很长，远端直接与臀鳍条相接；后部的近端辐状骨则长短如常，与中间辐状骨相接。从各部支鳍骨的大小排列及位置判断，比耶鱼臀鳍前部的近端辐状骨很可能已与前部对应的中间辐状骨愈合。当前标本的前部近端辐状骨(pr1～14)有14根，后部近端辐状骨(pr15～22)有8根。此外，在后部近端辐状骨之后另有一块很小的辐状骨骨板(prp)。当前标本前部近端辐状骨之后的一列中间辐状骨(mr)共有12根，其形状与背鳍的中间辐状骨相同。

尾鳍　当前标本的尾鳍(cf)强大，叉裂很深，上叶仅略微长于下叶，外形近呈正型尾。尾上叶背缘有一列硕壮的背棘鳞(dcf)，至少12枚；尾下叶前端可能发育有1枚腹棘鳞(vcf)，但远较背棘鳞短小。尾下叶前缘有近20根依次加长的分节鳍条，尾鳍鳍条总数在目前惟一的标本上难以计得，估计应多于60根。所有鳍条除基部一段外均分节，节长远大于节宽；前缘依次加长的鳍条不分叉，其余鳍条在远端分叉。

因尾上叶侧面大部为鳞片覆盖，尾鳍支鳍骨在当前标本上仅能观察到末端略膨大的脉棘和前面的6个尾下骨。当前标本上共有7根脉棘参与支持尾鳍；最后一根脉棘支鳍骨一般称为副尾下骨(phy)，尾动脉和尾静脉由此向后分为两支。尾下骨(hy)较脉棘支鳍骨宽短，以第一根最为宽大，往后依次减小。

鳞与侧线　与鲟形目的化石类群软骨硬鳞鱼及北票鲟相似，比耶鱼除尾上叶外，身体

两侧的硬鳞已完全退化消失；体侧惟一可见的骨化成分是头后侧线 (llcn)，骨化为管状小骨的头后侧线与鱼类的鳞片并不相同(Jin，1999)。

当前标本尾上叶侧面的硬鳞较为发育，鳞列前缘可达由后往前第 9 根脉棘的基部；但所有的硬鳞均细长，且无关节突和凹。

2　比较讨论

当前的标本体型细长，体侧裸露无鳞，脊椎弓片的骨化程度较高，尾部具有单个的神经棘，背鳍和臀鳍位处身体的后部，两者的鳍条数目均多于 50 根，臀鳍的近端辐状骨可分为前后两部分，而且近端辐状骨系列的后端有辐状骨愈合而成的骨板，尾鳍深分叉，上、下叶近等长，与比耶鱼科的特征完全吻合(Berg, 1940; Nielsen, 1949; Schwarz, 1970)，无疑可归入该科。

比耶鱼科目前仅包括比耶鱼一属。一度曾被归入比耶鱼科的无鳞鱼(*Psilichthys*)经重新研究后，发现其原本产自早白垩世地层，体侧并有圆鳞，与古鳕类的粒鳞鱼科(Coccolepididae)关系最为密切(Waldman,1971)。比耶鱼属的模式种是产自德国中三叠世壳灰岩的穆氏龙鱼(*Saurichthys mougeoti* Agassiz, 1834); Stensiö(1919)依据发现于斯匹次卑尔根早三叠世地层的该类化石，建立了比耶鱼属(*Birgeria*)。迄今，重新划归该属与陆续发现的比耶鱼已有 8 种(参见表 1)。此外，欧洲不少著名的三叠纪鱼类化石产地，以及俄罗斯西伯利亚勒拿河下游和美国内华达等地的三叠纪地层中亦有零星的比耶鱼未定种类报道。

表 1　比耶鱼属的已知种类与分布

Table 1　Species and distribution of *Birgeria* Stensiö, 1919

种(Species)	分布(Distribution)
Birgeria mougeoti (Agassiz, 1834)	欧洲中三叠统(Middle Triassic of Europe)
Birgeria groenlandica Stensiö, 1932	东格陵兰下三叠统(Lower Triassic of East Greenland)
Birgeria nielseni Lehman, 1948	马达加斯加下三叠统(Lower Triassic of Madagascar)
Birgeria aldingeri Schwarz, 1970	斯匹次卑尔根下三叠统(Lower Triassic of Spitsbergen)
Birgeria velox (Jordan,1907)	美国加州北部中三叠统(Middle Triassic of Northern California, USA)
Birgeria stensiöi Aldinger, 1931	瑞士南部中三叠统(Middle Triassic of Southern Switzerland)
Birgeria acuminata (Agassiz, 1844)	欧洲上三叠统(Upper Triassic of Europe)
Birgeria liui sp. nov.	中国华南上三叠统(Upper Triassic of South China)

国外已知的 7 种比耶鱼中，标本较为完整并经过详细研究的有 4 种：格陵兰比耶鱼(*B. groenlandica*)、尼氏比耶鱼(*B. nielseni*)、阿氏比耶鱼(*B. aldingeri*)和史氏比耶鱼(*B. stensiöi*)。其余 3 种，包括原来作为模式种的穆氏比耶鱼(*B. mougeoti*)，均由 Stensiö(1919,1921,1932)从其他科属划入比耶鱼，但这 3 种比耶鱼所依据的化石都较零散，而且原始记述十分简略，在后来有关比耶鱼的论著中大多仅是提及而已。Stensiö(1921)曾把斯匹次卑尔根早三叠世的比耶鱼化石归入模式种加以详细描述；Schwarz (1970)在深入研究史氏比耶鱼后，将斯匹次卑尔根的标本重新划归新建的阿氏比耶鱼。

中国新发现的标本虽然仅保存了身体的后部，但以其更显细长的体型、相对靠前的背

鳍和臀鳍、以及更为强大的尾鳍等特征，与早三叠世的比耶鱼化石易于区别(参见 Stensiö, 1921,1932;Nielsen, 1949; Lehman, 1948, 1952)。在已知的比耶鱼中，当前标本与史氏比耶鱼最为相近，两者在身体后部的形态特征上颇为相似，当前标本仅在尾柄长高之比、尾鳍长短与上下叶外缘交角、背鳍和臀鳍辐状支鳍骨的数目、臀鳍近端辐状骨骨板的大小、以及侧线管骨化与否等特征上与史氏比耶鱼略有差异(表 2)。比耶鱼不同种类之间的区别主要反映在头骨特征上，相信随着标本的增多，中国新发现的比耶鱼与史氏比耶鱼在头骨特征上亦应有所区别。因此，笔者将当前的标本命名为刘氏比耶鱼(*Birgeria liui* sp. nov.)。

表 2 刘氏比耶鱼(新种)与史氏比耶鱼身体后部形态特征的比较

Table 2 Comparision between *Birgeria liui* sp. nov. and *Birgeria stensiöi* Aldinger, 1931

特征(Characters)	*Birgeria liui*	*Birgeria stensiöi**
尾柄长/尾柄高(caudal peduncle length/caudal peduncle depth)	2.7	2.6
尾鳍长/尾柄长(caudal fin length/caudal peduncle length)	1.9	1.6
尾鳍上下叶外缘交角(intersecting angle of the dorsal and ventral margins of the caudal fin)	70°	65°
尾部脊椎弓片及体节(precaudal vertebral ossifications or metameres in the caudal region)	36	36
背鳍起点相对的尾前体节(precaudal metamere opposite to the commencement of the dorsal fin)	29th	29th
背鳍近端独立的辐状支鳍骨(autogenous proximal radials of the dorsal fin)	14	12
背鳍中间辐状支鳍骨(middle radials of the dorsal fin)	ca. 30～32	>17
臀鳍起点相对的尾前体节(precaudal metamere opposite to the commencement of the anal fin)	22nd	21st
臀鳍前部与后部独立的近端辐状支鳍骨(anterior long radials and posterior normal autogenous proximal radials of the anal fin)	14; 8	16; 7
臀鳍中间辐状支鳍骨(independent middle radials of the anal fin)	12	>7
臀鳍近端辐状骨骨板(proximal radial plate of the anal fin)	很小(very small)	较大(larger)
尾鳍上下叶棘鳞(dorsal and ventral caudal fulcra)	>12;1	14;1
侧线管小骨(lateral line canal ossifications)	有(present)	未见(absent)

* 史氏比耶鱼最为完好的标本是 Schwarz(1970)研究的 Val Porina 标本，但 Schwarz 的描述有不少明显与标本不符之处，故而该种的特征主要依据对这一标本各部照片的重新观察。(The specimen of Val Porina is the most complete representative of *B. stensiöi*. But its description by Schwarz, 1970 appears not well consistent with the specimen, so the characters of this species compared here are mainly after observations on the well-taken photos of the specimen in the paper.)

比耶鱼最初归于古鳕科(Palaeoniscidae)；1937 年，Aldinger 在重新厘定古鳕科时，建立了比耶鱼科，并将其划归软骨硬鳞鱼类，与匙吻鲟科(Polyodontidae)并列为一组(Aldinger, 1937:p. 377)。嗣后，比耶鱼作为原始辐鳍鱼类独立的一科已得到公认，但对比耶鱼科的系统位置尚有不同的认识。主导的两类观点一是仍将其归置于古鳕类(如 Berg, 1940; Lehman, 1958; Schwarz, 1970)；另一类观点则认为比耶鱼与匙吻鲟的关系密切，如

Nielsen曾列举了两者之间的14个异同演变特征，将比耶鱼视为匙吻鲟演化序列的侧支(Nielsen, 1949: 292～294)。比耶鱼的体侧裸露，仅有骨化的管状侧线，宽大的副蝶骨末端伸达头后，鳃盖骨退化，尾鳍叉裂深，上、下叶近等长，在原始辐鳍鱼类中与鲟形目鱼类(Acipenseriformes)最为相近。但是，比耶鱼也具有不少的特有特征，如颊部有一列细长的次眶骨、下鳃盖骨由4～6块三角形的骨片组成、尾部的成对神经棘已合而为一。因此，比耶鱼很可能即为鲟形目的姊妹类群；笔者在此新建比耶鱼目(Birgeriiformes ord. nov.)，这一新目与鲟形目同属Patterson(1982)重新厘定以后的软骨硬鳞鱼超目(Chondrostei)。

比耶鱼是仅见于三叠纪海相地层的大型肉食性鱼类，已知最大个体全长可达2m。比耶鱼体呈纺锤型，体侧光滑，尾鳍深叉形，尾柄细而有力，推测应为具有快速游泳能力的大洋性鱼类；成年个体可能洄游至近岸海域或由生物礁环绕而成的海盆中产卵；部分种类还很有可能是卵胎生(参见Schwarz, 1970; Beltan, 1996)。

在已知的比耶鱼中，云南罗平新发现的刘氏比耶鱼与史氏比耶鱼最为相近，后者产自瑞士南部圣乔治山(Monte San Giorgio)中三叠世安尼西与拉丁期交界的边境沥青层(Grenzbitumen-horizon, ＝贝萨诺组Besano Formation)，从而再次表明华南扬子区中、晚三叠世鱼类化石与特提斯西部鱼群密切的动物地理关系。苏德造早年记述的东方肋鳞鱼、贵州中华真颚鱼和兴义亚洲鳞齿鱼亦发现自法郎组竹杆坡段(据Su, 1959; Wang et al., in press)，这3种鱼类化石与意大利伦巴第(Lombardy)和瑞士圣乔治山等地相近时期的肋鳞鱼、真颚鱼和半椎鱼类均颇为相似(参见Brough, 1939; Tintori and Lombardo, 1999; Bürgin, 1999)。随着华南扬子区更多三叠纪鱼类化石和海生爬行动物的发现与研究的深入，必将进一步明确华南扬子区与其他地区的动物地理关系。

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NOTES ON THE DISCOVERY OF *BIRGERIA* IN CHINA

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Key words Luoping of Yunnan, early Late Triassic, Falang Formation, Birgeriidae

Summary

An incomplete specimen of *Birgeria* is described in the present paper, which is from the early Late Triassic Zhuganpo Member of the Falang Formation in Luoping of Yunnan Province, South China. Although this new specimen is lack of skull and anterior part of the body, its preserved characters are in well agreement with the diagnoses of *Birgeria*: A large fusiform fish about 800 mm in total length; peduncle slender; body naked without scales and bony plates except on the upper lobe of the caudal fin; vertebral elements ossified, paired basidorsals and basiventrals in the caudal region, except the anteriormost

10 pairs of basidorsals, fused with each other distally as single neural spines and haemal spines; dorsal and anal fins situated backward, anal fin slightly farther back than the dorsal fin, both with more than 50 fin rays; pterygiophores of the dorsal and anal fins with two series of ossifications: proximal and middle radials; proximal pterygiophore series of the anal fin including anterior long radials and posterior normal radials, at the end of this series with a small plate evidently co–ossified from the posteriormost proximal radials; caudal fin deeply cleft and nearly equilobate, with well developed dorsal caudal fulcra and more than 60 fin rays; scales on the upper caudal lobe long and narrow, without peg–and–socket articulation.

Among the known species of *Birgeria*, the specimen discovered for the first time in China is steadily distinctive from the Early Triassic forms (*B. groenlandica, B. nielseni, B. aldingeri*) in its slender caudal peduncle and longer caudal region (the peduncle length is 2.7 times of its depth, and there are 36 metameres in the caudal region besides those in the caudal fin), relatively forward dorsal and anal fins (the commencement of the dorsal and anal fins is opposite to the 29th and 22nd precaudal metameres respectively), and more stronger caudal fin (the dorsal and ventral margins of the caudal fin intersect in 70°); whereas the new specimen is quite similar to the Middle Triassic *B. stensiöi* from Grenzbitumen–horizon of Monte San Giorgio in southern Switzerland. At present, the Chinese specimen is only discriminated from *B. stensiöi* by minor differences in the caudal region: ratio of the caudal peduncle length to the depth, length of the caudal fin and its intersecting angle of the dorsal and ventral margins, number of the pterygiophores of the dorsal and anal fins, size of the proximal radial plate of the anal fin, and lateral line canal ossifications. It is justified to assume that there must be some differences in the skull between the Chinese specimen and the Switzerland species of *Birgeria* because the known species of this genus are mainly distinguished by the characters from head skeletons. Hence, the Chinese specimen is assigned to a new species – *B. liui* sp. nov. The species name is in honor of the Chinese paleoichthyologist LIU Xian–Ting (LIU Hsien–T'ing), who passed away at the beginning of this new millennium.

The systematic position of the monogeneric family Birgeridae is yet to be revised using the phylogenetic principles. Traditionally, Birgeridae was referred to Palaeonisciformes or to Chondrostei as a side–branch of the polyodontid fishes. Among the lower actinopterygian fishes, Birgeridae is most closely related to Acipenseriformes, especially to the fossil acipenseriform families Chondrosteidae and Peipiaosteidae. At least, Birgeridae and Acipenseriformes share the following characters: body naked without scales and bony plates except on the upper caudal lobe, broad parasphenoid extending backward beyond the posterior end of endocranium, opercle reduced, caudal fin deeply cleft and nearly equilobate. On the other hand, birgerid fishes possess quite a few peculiar features, e. g. a series of 8～11 long and narrow suborbitals, subopercle consisting of 4～6 triangular plates, neural spines singular in the caudal region, and they are most probably representatives of another clade apart from Acipenseriformes in the present superorder Chondrostei, which is newly named as Birgeriiformes.

Birgeria liui sp. nov., and the previously known fossil fishes (*Peltopleurus orientalis*, *Sinoeugnathus kueichowensis*, and *Asialepidotus shingyiensis*) from the same horizon in the nearby Xingyi of Guizhou Province as well, are all closely related to the respective fishes from Monte San Giorgio of Switzerland and Lombardy of Italy. Most Middle and early Late Triassic marine reptiles discovered from South China also show a similar systematic pattern. This congruent pattern of piscine and reptilian phylogeny indicates that nowaday South China and Southern Alps might be closely related biogeographically during the Middle and early Late Triassic time.

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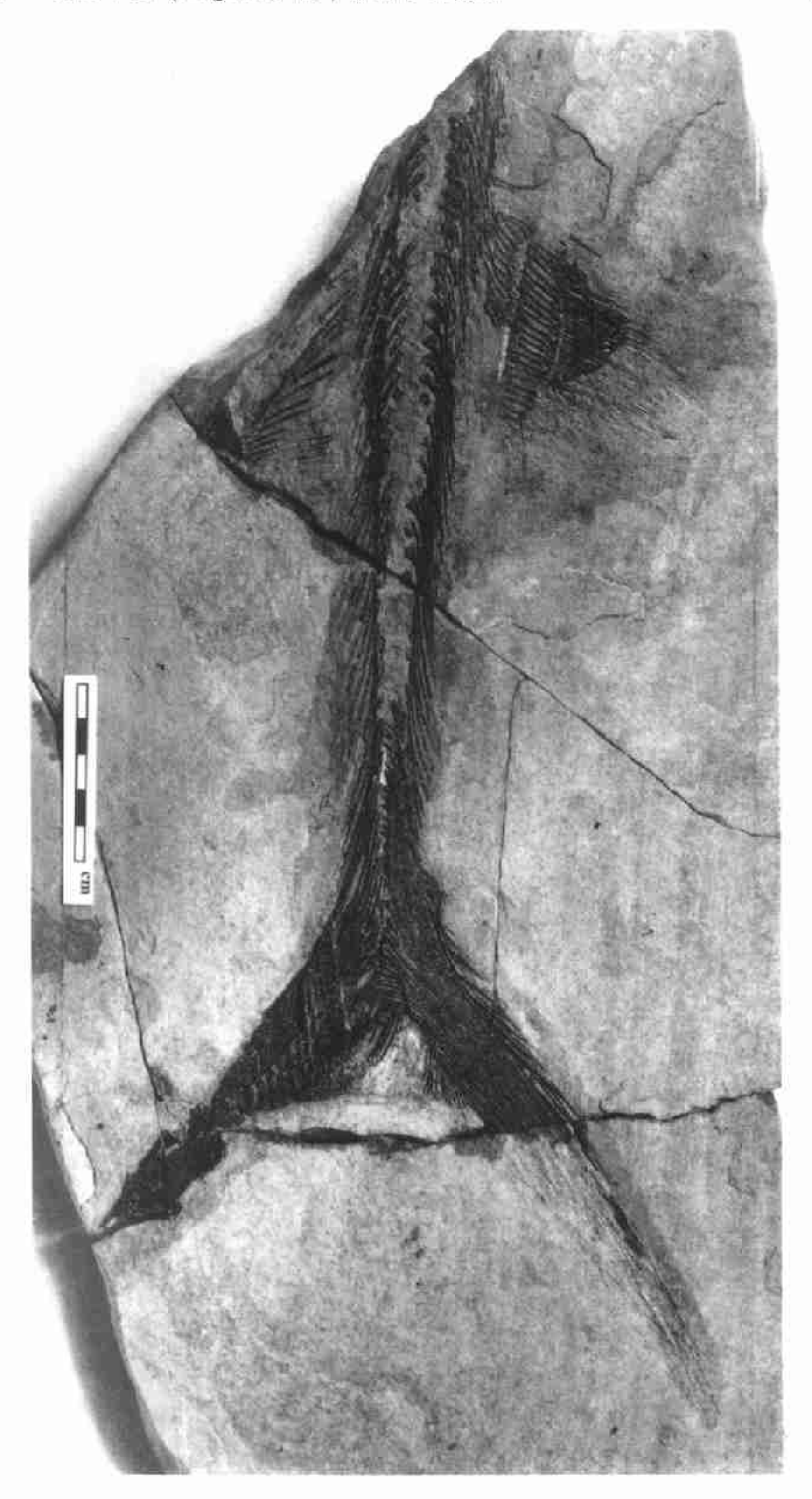
图版说明 (Explanations of plates)

图版 I (Plate I)

Birgeria liui sp. nov., 正型标本(holotype; IVPP V 12569A)

图版 II (Plate II)

Birgeria liui sp. nov., 正型标本的负模(counterpart of the holotype; IVPP V 12569B)


cm


cm